Contributed Paper

Ants as a Measure of Effectiveness of Habitat Conservation Planning in Southern California

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Abstract: *In the United States multispecies habitat conservation plans were meant to be the solution to conflicts between economic development and protection of biological diversity. Although now widely applied, questions exist concerning the scientific credibility of the conservation planning process and effectiveness of the plans. We used ants to assess performance of one of the first regional conservation plans developed in the United States, the Orange County Central-Coastal Natural Community Conservation Plan (NCCP), in meeting its broader conservation objectives of biodiversity and ecosystem-level protection. We collected pitfall data on ants for over 3 years on 172 sites established across a network of conservation lands in coastal southern California. Although recovered native ant diversity for the study area was high, site-occupancy models indicated the invasive and ecologically disruptive Argentine ant (*Linepithema humile*) was present at 29% of sites, and sites located within 200 m of urban and agricultural areas were more likely to have been invaded. Within invaded sites, native ants were largely displaced, and their median species richness declined by more than 60% compared with uninvaded sites. At the time of planning, 24% of the 15,133-ha reserve system established by Orange County NCCP fell within 200 m of an urban or agricultural edge. With complete build out of lands surrounding the reserve, the proportion of the reserve system vulnerable to invasion will grow to 44%. Our data indicate that simply protecting designated areas from development is not enough. If habitat conservation plans are to fulfill their conservation promise of ecosystem-level protection, a more-integrated and systematic approach to the process of habitat conservation planning is needed.*

Keywords: ants, biodiversity, edge effect, habitat conservation planning, invasion, *Linepithema humile*, non-native species, southern California

Hormigas como una Medida de la Efectividad de la Planificación de la Conservación del Hábitat en el Sur de California

Resumen: *En los Estados Unidos se pensó que los planes de conservación de hábitat para múltiples especies eran la solución a los conflictos entre el desarrollo económico y la protección de la diversidad biológica. Aunque ampliamente aplicados en la actualidad, existen preguntas sobre la credibilidad científica del proceso de planificación de conservación y la efectividad de los planes. Utilizamos hormigas para evaluar el funcionamiento de uno de los primeros planes regionales de conservación desarrollado en los Estados Unidos, el Plan de Conservación de la Comunidad Natural en la Costa Central del Condado de Orange (NCCP), en el cumplimiento de sus objetivos generales de conservación en la protección de biodiversidad y el ecosistema. Recolectamos datos de hormigas durante más de tres años en 172 sitios establecidos en una red de tierras conservación en la costa del sur de California. Aunque la diversidad de hormigas nativas recuperada en el área de estudio fue alta, los modelos de ocupación de sitios indicaron que la especie de hormiga argentina invasora y ecológicamente perturbadora (*Linepithema humile*) estuvo presente en 29% de los sitios, y sitios localizados a 200 m de áreas agrícolas y urbanas tuvieron mayor probabilidad haber sido invadidos. En los sitios invadidos, las hormigas nativas fueron desplazadas, su riqueza de especies promedio declinó en más*

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de 60% en comparación con sitios no invadidos. Al tiempo de la planificación, 24% del sistema de reserva de 15133 ha establecido por el NCCP del Condado de Orange quedó a 200 m de un borde urbano o agrícola. Con la construcción en todos los terrenos que rodean a la reserva, la proporción del sistema de reserva vulnerable a la invasión incrementará a 44%. Nuestros datos indican que la simple protección de áreas designadas para desarrollo no es suficiente. Si los planes de conservación de hábitat han de cumplir su promesa de protección a nivel de ecosistema, se requiere que el proceso de planificación de la conservación de hábitat sea más integral y sistemático.

Palabras Clave: biodiversidad, efecto de borde, especies exóticas, hormigas, *Linepithema humile*, planificación de la conservación de hábitat, sur de California

Introduction

The use of habitat conservation plans (HCPs) to resolve conflicts between economic development and conservation of endangered species in the United States has grown rapidly since the U.S. Congress in 1982 added a provision (section 10[a][1][B]) to the Endangered Species Act to allow the wildlife agencies (U.S. Fish and Wildlife Service and National Oceanic and Atmospheric Administration Fisheries) to issue permits for the incidental take of listed species. In California wildlife agencies have expanded conservation planning beyond traditional single-species HCPs, favoring creation of comprehensive, multispecies conservation plans that meet the requirements of both federal HCPs and state natural community conservation plans (NCCPs). At present there are 32 active NCCPs covering more than 2.8 million ha in the state (CDFG 2008).

The primary objective of the NCCP program is to conserve biological communities at the ecosystem scale while permitting "compatible land uses" (CDFG 1991; USFWS 1996). Although the idea of a broad-based ecosystem approach to planning appeals to conservation biologists (Noss 1983; Possingham et al. 2001) and is followed elsewhere in the world (Pressey et al. 2007), reviews of the scientific quality of approved multispecies conservation plans have highlighted an absence of science in the planning process and raised questions about effectiveness of the plans in protecting biodiversity and the ecological functions of biological communities (Harding et al. 2001; Clark & Harvey 2002; Rahn et al. 2006; Hierl et al. 2008). With implementation of the first multispecies conservation plans now years underway, the opportunity to use empirical data to test the ability of regional conservation plans to protect biodiversity and ecosystem processes is beginning to emerge (Winchell & Doherty 2008).

Ants are valuable indicators for measuring environmental change and ecosystem functioning (Andersen & Majer 2004; Underwood & Fisher 2006; Fagan et al. 2008). They are surface and subterranean predators of small arthropods, generalist scavengers, granivores, detritivores, leafcutters that farm fungus, and tenders of aphids and scale insects (Hölldobler & Wilson 1990). Ants perform a variety of ecological functions in terrestrial ecosystems, including keystone functions such as the cycling of nutrients and organic matter, turning over soil, seed dispersal, and predation and scavenging of small animals (e.g., Hölldobler & Wilson 1990; Folgarait 1998; MacMahon et al. 2000). Ants' sheer numbers and great diversity worldwide make them significant ecological components for most terrestrial communities (Hölldobler & Wilson 1990) and support their selection as useful indicators for measuring performance of regional habitat conservation plans in protecting biodiversity and ecosystem processes.

In California the ant fauna exhibits considerable diversity and regional endemism. In total, 281 species in 44 genera have been identified in the state. Thirty-nine of the species, or 15% of the total native ant fauna, are endemic (Ward 2005). Within this fauna, introduced species are also present. Twenty-six introduced species have been identified within the state, most of which are confined to disturbed sites at low elevations (Ward 2005). One of the most ecologically important introduced ant species in California is the Argentine ant (*Linepithema humile*). Native to northern Argentina and surrounding regions (Wild 2004), *L. humile* has invaded areas with suitable climates, especially Mediterranean-type ecosystems, worldwide (Suarez et al. 2001; Tsutsui et al. 2001). In invaded landscapes, Argentine ants are restricted primarily to disturbed areas, but they can invade natural areas through the wildland–urban interface (Suarez et al. 1998, 2001). Where Argentine ants are present, the aboveground native ant fauna is often displaced (Ward 1987; Human & Gordon 1996; Suarez et al. 1998). This displacement is presumed to lead to the disruption of a number of key ecological processes within invaded terrestrial communities (Holway et al. 2002; Holway & Suarez 2006).

We examined the aboveground ant diversity for a large region of coastal southern California to evaluate effectiveness of one of the first regional HCPs developed in the United States—the Orange County Central-Coastal NCCP—in meeting its broader conservation goals of protecting regional biodiversity and ecosystem functioning. This multiple-species conservation plan was approved by U.S. wildlife agencies in 1996 and created a 15,133-ha reserve system within an 84,211-ha planning area in coastal southern California (Fig. 1). At the time of approval, the plan was considered a model for ecosystem-level conservation planning in the United States (Noss et al. 1997).

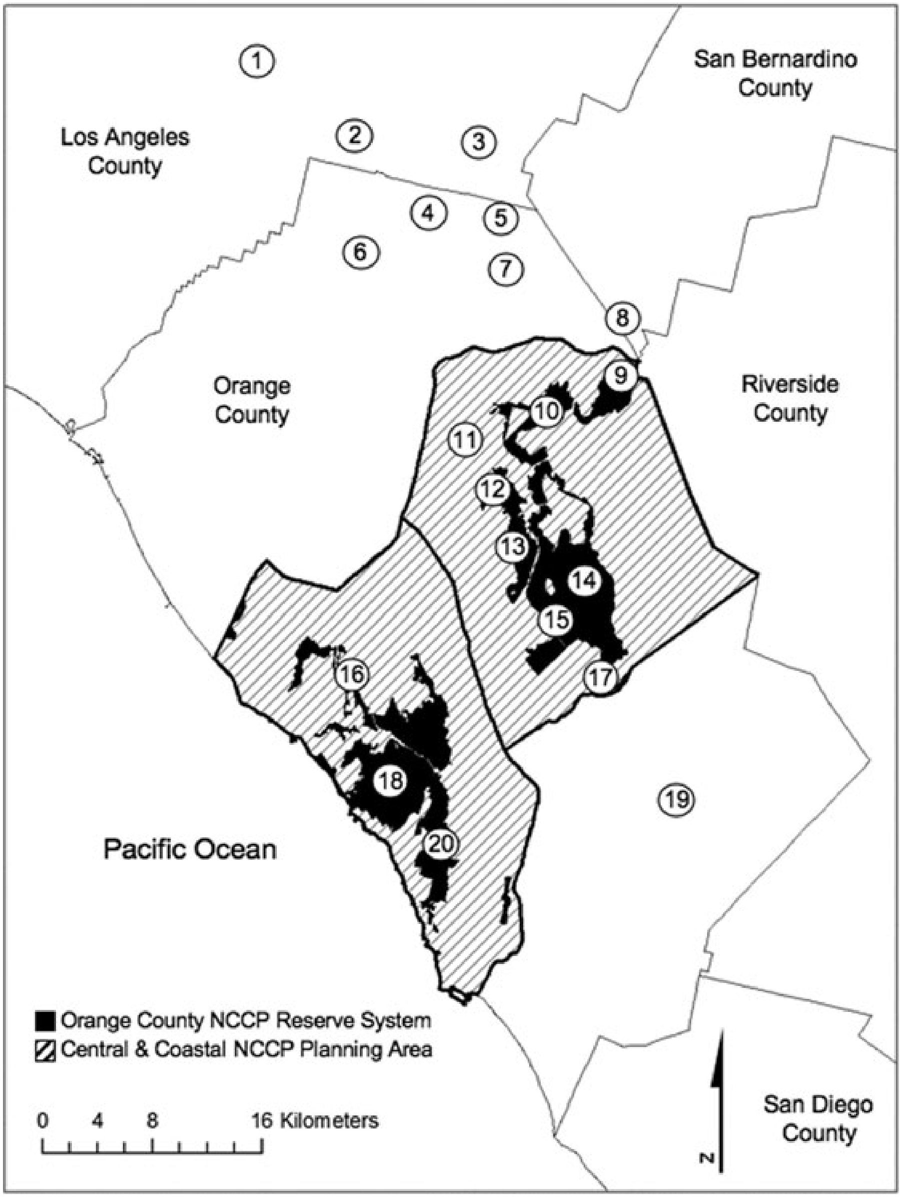

Figure 1. Geographic areas (numbered circles) sampled for ants in coastal southern California. Central and Coastal Natural Community Conservation Plan (NCCP) planning area is 84,211 ha. Locality information for individual geographic areas (area number, area name, county, number of sites): (1, Puente Hills 1, Los Angeles, 8; 2, Puente Hills 2, Los Angeles, 4; 3, Puente 3, Los Angeles, 3; 4, Puente Hills 4, Orange, 4; 5, Chino Hills State Park 1, Orange, 3; 6, Unocal, Orange, 3; 7, Chino Hills State Park 2, Orange, 13; 8, Chino Hills State Park 3, San Bernardino, 9; 9, Coal Canyon, Orange, 7; 10, Weir Canyon, Orange, 12; 11, Orange Hills, Orange, 5; 12, Peters Canyon Regional Park, Orange, 5; 13, Rattlesnake Reservoir, Orange, 5; 14, Limestone Canyon, Orange, 19; 15, Agua Chinon, Orange, 7; 16, UC Irvine Ecological Preserve, Orange, 5; 17, Southern California Edison Parcel, Orange, 5; 18, San Joaquin Hills, Orange, 21; 19, Audubon Starr Ranch Sanctuary, Orange, 17; 20, Aliso & Wood Canyons Wilderness Park, Orange, 17.

Specifically, we catalogued and examined native ant diversity across a large regional network of conservation lands that includes the entire reserve system established by the Orange County NCCP; measured the spatial patterns of Argentine ant invasion across the urban–wildland interface present within the network; evaluated subsequent changes in native ant diversity following invasion; and on the basis of recovered spatial patterns, used GIS to assess past and future vulnerability of the reserve system to invasion by Argentine ants.

Methods

Over a 40-month period from October 1999 through January 2003, we sampled 172 sites distributed across 20 geographic areas in a network of conservation lands located in the foothill and lowland regions of coastal southern California (approximately 1500 km^2; Fig. 1). Of the 172 sites, 63% were in the Orange County NCCP reserve system (geographic areas 9–18, 20). Within each geographic area, individual sites were present largely in sage scrub habitats and stratified across a range of distances from urban and agricultural edges. Site locations were selected in association with coastal locations of pitfall arrays sampled as part of a U.S. Geological Survey (USGS) monitoring project designed to collect baseline data on the distribution of reptiles and amphibians across southern California (Fisher & Case 2000).

An individual site consisted of five pitfall traps placed in a pattern resembling the five on a die, with corner traps spaced 20 m apart. Compared with other census techniques (e.g., nest counting or bait traps), pitfalls provide better estimates of species richness because they operate by themselves, operate continuously, and are not biased by differential attractiveness (Andersen 1997; Bestelmeyer et al. 2000). We used pitfall traps that were 28 mm in diameter, 115 mm deep, 50-mL plastic centrifuge tubes partially filled with propylene glycol (i.e., antifreeze; Suarez et al. 1998). We nested the traps in 32.5-mm-diameter PVC pipe buried at ground level, so the top of the tube was flush with the ground surface (Majer 1978). Traps were deployed for 10 consecutive days per collection period or sample occasion. After the 10 days, pitfall traps were transported to the laboratory and the contents were sorted and identified and voucher specimens were selected. We counted only worker ants. We noted winged queens and males, but did not use them in analyses because they could have originated from outside the sampling locations. As necessary, specimen vouchers were sent to taxonomic experts for confirmation of species identity (see Supporting Information). We held sampling effort relatively constant throughout the study period with individual sites sampled approximately every 6 months, with a mean (SD) total of 6.8 (0.9) sample occasions for the study. Compiled data represented 1161 sample occasions or 58,050 individual trap nights. In a different context, a subset of the pitfall data was analyzed by Menke et al. (2007, 2008).

To compare the distribution of native ant species across sites, we constructed likelihood-based models of site occupancy for the top 12 most-frequently detected native ant species with program PRESENCE (MacKenzie et al. 2002). PRESENCE estimates the proportion of area occupied by a species of interest. Because species are not always detected even when present at a site, naïve estimation of the total area occupied tends to underestimate the true distribution of a species. Through repeated surveying of sites, the probability of detecting species can be estimated, which then allows unbiased estimation of the proportion of area occupied (MacKenzie et al. 2002). The construction of occupancy models required us to convert count data into a matrix of 1s and 0s (1, species detection; 0, no detection) for each individual species. Resulting matrices were each 172 (the number of sites) by 22 (the total number of unique sample occasions for the entire study) cells in size. To assess the importance of Argentine ants in explaining the recovered patterns of occupancy, we included observed presence or absence of Argentine ants as a site-specific covariate in each of the 12 single-species models.

To assess the distribution of Argentine ants across the study area, we expanded the occupancy model used in analysis of the native ant data to include estimation of local extinction probabilities (MacKenzie et al. 2003) and site-specific covariates. Site covariates allowed us to evaluate the importance of edge effects and watercourses in explaining occupancy patterns. We used 2002 Land Cover GIS data (California Department of Forestry & Fire Protection) to calculate the distance between individual sites and the nearest urban or agricultural edge or watercourse. We delineated four categorical variables that differentiated sites located within and beyond 100, 200, 300, and 500 m of urban or agricultural edges and a single variable (riparian) that differentiated sites within and beyond 50 m from mapped watercourses for use as site-specific covariates. We compared competing occupancy models by ranking the candidate set according to Akaike's information criterion (AIC) (Akaike 1973) and model averaged the parameter estimates (i.e., site occupancy, local extinction, and detection probability) with Akaike weights (w_i) to derive a weighted average.

We measured displacement of native ants following invasion by Argentine ants in three ways. We tested for the relationship between proportion of sites occupied by Argentine ants and native ant species richness across geographic areas with least-squares linear regression. We used the Mann-Whitney test to check for differences in number of native ant species present at sites occupied and unoccupied by Argentine ants. At sites where Argentine ants were detected, we used a one-way analysis of variance to compare differences in native ant species richness among sites on the basis of Argentine ant abundance. Finally, to generate a measure of the reserve system's vulnerability to Argentine ant invasion at the time of formation, we used GIS Land Cover data developed in 1992 (County of Orange, Planning Division) to measure total mapped area of the reserve located within a specified distance (defined by the highest-ranking Argentine ant occupancy model) from the edge of urban and agricultural areas. To estimate future vulnerability of the Orange County reserve system following complete build out of the lands surrounding the reserve, we measured the total mapped area of the reserve located within the specified distance from the reserve system's established boundaries.

Results

In total, 83,288 ants, representing 53 native ant species in 24 genera and three introduced species (*L. humile*, *Cardiocondyla ectopia*, and *Monomorium pharaonis*) were collected and identified during the study (Supporting Information). The number of native ant species detected was 21% of the total native ant species and 55% of the genera that occur in California. The distribution of different ant species varied widely across the study area. For the top 12 captured native species, individual distributions ranged from 16% to 83% of the total number of sampled sites (Fig. 2a). Naïve estimates of occupancy, for most species included in the modeling process, closely matched model estimates (Fig. 2a). This is not surprising given that naïve estimates were derived

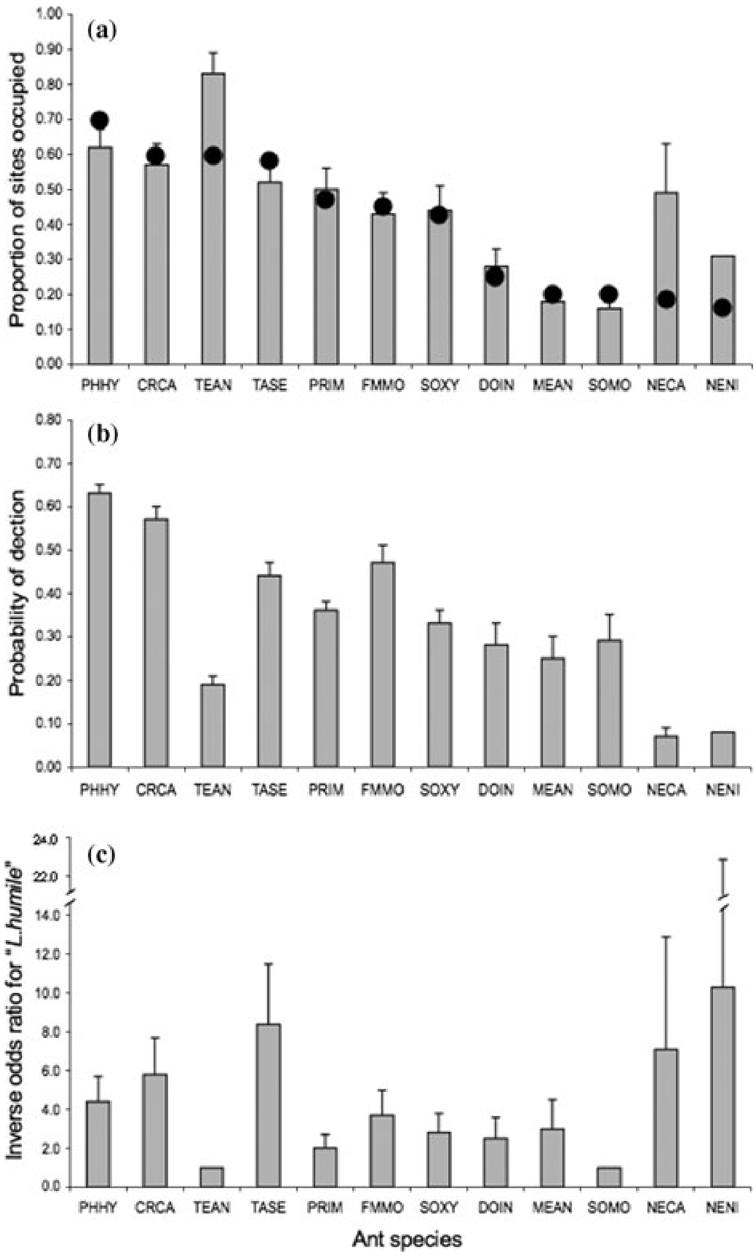

Figure 2. (a) Naïve estimates (dark circles) and estimates of site occupancy (1 SE) for the 12 most widely detected native ant species. (b) Probability of detection (1 SE) for the 12 ant species as estimated by program PRESENCE. (c) Species-specific sensitivity of ants to the presence of Argentine ants as indicated by the inverse odds ratio (1 SE) for the covariate L. humile *calculated in program PRESENCE. A value of 1.0 indicates no observed sensitivity to* L. humile *(i.e., model with the presence or absence of* L. humile *included as a site covariate did not rank higher than models that did not take into account the distribution of* L. humile*). A value of 10.0 indicates a species is 10 times less likely to be present at sites where* L. humile *was detected than in sites where* L. humile *was not detected. Abbreviations: PHHY,* Pheidole hyatti*; CRCA,* Crematogaster californica*; TEAN,* Temnothorax andrei*; TASE,* Tapinoma sessile*; PRIM,* Prenolepis imparis*; FMMO,* Formica moki*; SOXY,* Solenopsis xyloni*; DOIN,* Dorymyrmex insanus*; MEAN,* Messor andrei*; SOMO,* Solenopsis molesta*; NECA,* Neivamyrmex californicus*; and NENI,* Neivamyrmex nigrescens*).*

from an exceptionally large number of sample occasions. Naïve estimates of site occupancy for *Temnothorax andrei*, *Neivamyrmex californicus*, and *Neivamyrmex nigrescens*, were much lower than modeled estimates. Although sample sizes were large, the low rates of detection of each of these species (mean probability of detection [SE]: 11% [4]; Fig. 2b) relative to the other most commonly captured species (40% [5]) apparently led to the discrepancy between estimates. Sensitivity to the presence of Argentine ants was not consistent across native species (Fig. 2c). Of the 12 most widely distributed native ants, *N. californicus, N. nigrescens*, *Tapinoma sessile*, *Crematogaster californica*, and *Pheidole hyatti* were the most sensitive to the presence of Argentine ants, whereas *T. andrei*, *Solenopsis molesta*, *Prenolepis imparis*, and *Dorymyrmex insanus* were the least sensitive.

We detected Argentine ants in 17 of 20 geographic areas and 58 of 172 surveyed sites (naïve estimate of site occupancy: 34%). The highest-ranking occupancy model for the Argentine ant included the site-specific covariate 200 m from urban or agricultural areas (Table 1). This model showed there was a 75% chance that sites located within 200 m of an urban or agricultural area were occupied by Argentine ants. Beyond 200 m, the probability of occupancy dropped to 10%. Whether or not watercourses were present within 50 m of survey sites was not important when included as the sole site covariate in the model or when distance to the urban or agricultural edge was already included in the model (i.e., AIC score

Table 1. Summary of the model-selection procedure and parameter estimates (1 SE) for the Argentine ant (*Linepithema humile*).

Model[a]	*Δ AIC*[b]	w_i[c]	K[d]	$\hat{\psi}$	$\hat{\varepsilon}$	$\hat{p}$
ψ(200 m)ε(·)*p*(·)	0.00	0.69	4	0.29 (0.01)	0.09 (0.03)	0.76 (0.02)
ψ(200 m, Riparian)ε(·)*p*(·)	1.64	0.31	5	0.29 (0.01)	0.09 (0.03)	0.76 (0.02)
ψ(300 m)ε(·)*p*(·)	17.06	0.00	4	0.29 (0.01)	0.08 (0.02)	0.76 (0.02)
ψ(400 m)ε(·)*p*(·)	17.33	0.00	4	0.29 (0.01)	0.08 (0.02)	0.76 (0.02)
ψ(500 m)ε(·)*p*(·)	27.10	0.00	4	0.29 (0.01)	0.08 (0.02)	0.76 (0.02)
ψ(100 m)ε(·)*p*(·)	50.23	0.00	4	0.29 (0.03)	0.08 (0.02)	0.76 (0.02)
ψ(·)ε(·)*p*(·)	83.84	0.00	3	0.29 (0.03)	0.08 (0.02)	0.76 (0.02)
ψ(Riparian)ε(·)*p*(·)	87.19	0.00	4	0.29 (0.05)	0.08 (0.02)	0.76 (0.02)
ψ(·)*p*(·)	196.16	0.00	2	0.17 (0.02)	0.00 (0.00)	0.78 (0.02)
Model-averaged estimates				0.29 (0.01)	0.09 (0.03)	0.76 (0.02)

[a] *Model parameters with associated covariates (in parentheses) include: ψ, occupancy; ε, extinction; and* p, *detection.*
[b] *Difference in Akaike's information criterion (AIC) values between each model and the low-AIC model. When comparing the relative fits of a suite of models, differences in AIC values among models indicate the relative support for different models.*
[c] *The AIC model weight. Weights have a probabilistic interpretation. Of these models,* w_i *is the probability that model* i *is selected as the best-fitting model if the data are collected again under identical conditions.*
[d] *Number of parameters in the model.*

increased when the site-covariate "riparian" was included in either model). The model-averaged estimate (SE) of annual site occupancy for the species was 29% (1), annual extinction rate (partially offset by an uncalculated colonization rate) was 9% (3), and probability of detection was 76% (2). The difference in the naïve and estimated occupancy rate was due to the estimated value being a measure of annual occupancy, whereas the naïve estimate was based on the number of sites where Argentine ants were observed throughout the study period.

Across geographic areas and between sites, the presence of Argentine ants was correlated with a diminished assemblage of native ants. Across geographic areas the average number of native ant species detected declined as the proportion of sites within each geographic area with Argentine ants increased (Fig. 3). Between sites, the number of native species at sites with *L. humile* was significantly lower than sites without *L. humile* (Fig. 4). At sites where Argentine ants were present, the native ant assemblage appeared sensitive to the level of Argentine ant abundance and declined in species richness as the abundance of Argentine ants increased (Fig. 5).

When we used 200 m from urban and agricultural edges as the distance variable that best explains Argentine ant presence within the network of sampled conservation lands, a large proportion of the reserve was vulnerable to invasion by Argentine ants. At the time of planning (circa 1992), the total area of the reserve system that fell within 200 m of an urban or agricultural edge was 3599 ha (or 24%). With complete build out of lands surrounding the reserve, 6592 ha (or 44%) of the total reserve system will be within 200 m of an urban or agricultural area.

Discussion

Unlike single-species HCPs, multispecies conservation plans aim to preserve biological diversity and ecosystem processes across a broad spectrum of habitats at the level of large landscapes (CDFG 1991; USFWS 1996). Due to high rates of species extirpation caused largely by habitat conversion and urban development, the exceptionally rich biological diversity of coastal southern California (Stebbins & Major 1965; Myers et al. 2000) is widely regarded as the most highly threatened in the United States (Tennant et al. 2001). Thus, habitat conservation planning at broad and fine scales has received much attention in this region. Our findings illustrate vulnerability of the

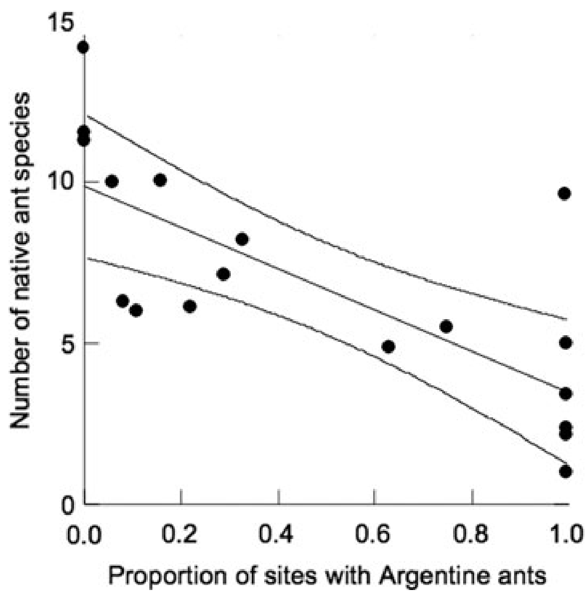

Figure 3. Proportion of sampled sites within a geographic area with Argentine ants detected relative to the average number of native ant species (with 95% CI). The formula for the regression line is number of native ant species = 9.884 − 6.41 × proportion of sampled sites with Argentine ants detected ($F = 24.48$*,* $p < 0.001$*,* $r^2 = 0.576$*,* $n = 20$*).*

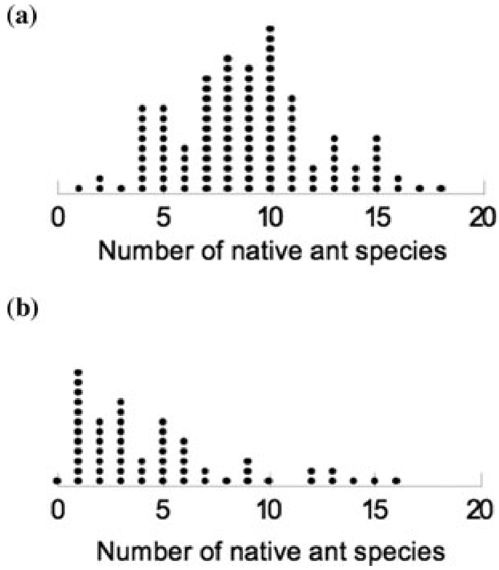

Figure 4. Differences in the distribution of the number of native ant species observed at sites (a) unoccupied (mean [SE] = 8.9 [0.3], median = 9.0) and (b) occupied (mean = 4.9 [0.5] and median = 3.5) by Argentine ants ($U = 5272.5$*,* $p < 0.001$*,* $n = 172$*).*

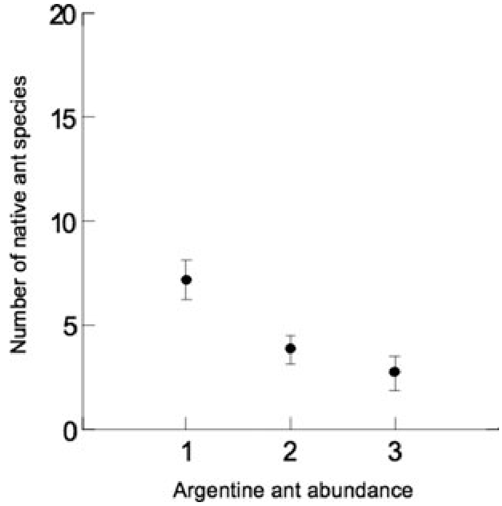

Figure 5. Native ant species richness (95% error bars) as a function of Argentine ant abundance: level 1, <1 average number of Argentine ants collected per 10-day sample period; level 2, ≥1 and <10; level 3, ≥10. Mean (SE) native ant species richness by Argentine activity: level 1, 7.2 (0.9), $n = 22$*; level 2, 3.8 (0.7),* $n = 26$*; level 3, 2.7 (0.8),* $n = 10$ *(*$F = 7.137$*,* $p < 0.01$*,* $n = 58$*).*

Orange County reserve system to invasion by Argentine ants. Although touted as a national model, the high levels of permitted urban and agricultural edge associated with the Orange County NCCP appear to limit the regional conservation plan in its ability to provide ecosystem-level protection to a large portion of its reserve system.

Argentine ants are invading natural areas through the wildland–urban interface. The high probability of Argentine ant presence within 200 m of an urban or agricultural edge shown in our work is reflected in smaller-scale studies. Within isolated habitat fragments (<100 ha) in urbanized areas of San Diego County (approximately 150 km south-southeast of our study area), the abundance of Argentine ants declines sharply as distance from the urban–scrub interface increases, and Argentine ants are rarely detected beyond 200 m from an urban edge (Suarez et al. 1998; Bolger et al. 2000). In contrast with the areas sampled in these earlier studies, more than 80% of the sites in our study were embedded in large, contiguous natural areas >2500 ha in size. The consistency in results given variation in size and configuration of the sampled areas between studies suggests invasion of natural areas by Argentine ants is an edge effect and not simply a byproduct of insularization of native habitat by urban development.

Although abundance of Argentine ants is positively associated with riparian corridors in other areas of California (Ward 1987) and patterns of occurrence at the local scale are strongly dependent on fine-scale differences in soil moisture (Holway 2005; Menke & Holway 2006; Menke et al. 2007), the presence of nearby watercourses failed as a predictor of the presence of Argentine ants in our study. One possible explanation for this is that unlike urban and agricultural edges, not all riparian areas are invaded. Because natural streams are largely ephemeral in coastal southern California, seasonal fluctuations in levels of soil moisture may limit the ability of Argentine ants to invade watercourses outside low-lying perennial streams that receive year-round runoff from nearby urban and agricultural areas. A second explanation is that our study design undersampled the upland areas immediately adjacent to riparian habitat to the extent that we could not detect a positive effect of riparian conditions. Holway (2005) describes a sharp drop off in Argentine ant abundance and level of soil moisture outside a riparian corridor. Thus, at 50 m from a watercourse Argentine ants may be uncommon enough for watercourses, as defined by this study, to fail as a good predictor of occurrence.

In agreement with the results of previous studies (Ward 1987; Suarez et al. 1998; Holway et al. 2002), we found the epigaeic (i.e., aboveground) native ant assemblage was largely being displaced at invaded sites. Median species richness of ants in invaded sites was over 60% lower than in uninvaded sites. Within invaded sites, native ants appeared sensitive to Argentine ant abundance because species richness dropped on average by over 60% between lightly and heavily invaded sites. The displacement of native ants, largely through the combined effects of interference and exploitative competition

(Human & Gordon 1996) and the direct raiding of nests (Ward 1987; Zee & Holway 2006), may result in ecological consequences for invaded landscapes (Holway et al. 2002). Within these landscapes, native ant species are differentially affected by the presence of Argentine ants.

In our study the dispersal-limited army ants, *N. californicus* and *N. nigrescens*, specialist predators of the brood of other ant species (Gotwald 1995), and the ecologically similar *T. sessile* appear to be the most sensitive to the presence of Argentine ants. For army ants, displacement of their prey base and their limited ability to recolonize invaded areas following extirpation is likely to explain much of their sensitivity to invasion. The four least-sensitive species identified by our study (*T. andrei, S. molesta, P. imparis*, and *D. insanus*) persist longest in invaded natural habitats in San Diego County (Suarez et al. 1998; Holway 2005) and other areas of California (Ward 1987). Temporal niche partitioning by *P. imparis* (Ward 1987), the parasitic association of *S. molesta* with other ants, including *L. humile* (Suarez et al. 1998), and the small size and cryptobiotic nature of *T. andrei* (Suarez et al. 1998) all effectively reduce competition for resources with Argentine ants and thus likely explain much of these species' resistance to invasion.

Because Argentine ants are difficult to control and nearly impossible to eradicate once established (Holway et al. 2002; Holway & Suarez 2006), the large and biologically diverse Orange County reserve system is expected to become less functional over time. The estimated total size of lands vulnerable to invasions by non-native ants ranges between 24% and 44%. Within invaded areas, loss of almost half the native ant diversity is predicted. In these areas, we expect a number of ecological functions performed by native ants to be compromised. Because ground-foraging ant species are disproportionately affected, entire functional groups are likely to be lost, and cascading effects are expected to increase in probability (Walker 1992). Evidence is beginning to emerge that suggests such effects may be in progress. In adjacent areas of southern California, presence of Argentine ants is linked to loss of coast horned lizards (*Phrynosoma coronatum*) (Fisher et al. 2002), desert shrews (*Notiosorex crawfordi*) (Laakkonen et al. 2001), and arthropod (Bolger et al. 2000) populations, and to disruption of seed-dispersal mutualisms involving the ant-dispersed *Dendromecon rigida* (Carney et al. 2003).

In the case of the coast horned lizard, the relationship between displacement of native ants and decline of the species appears especially clear. The coast horned lizard is a dietary specialist that feeds almost exclusively on native ants (Suarez et al. 2000). In invaded areas, horned lizards do not consume Argentine ants, but instead shift their diets to incorporate more species of arthropods (Suarez et al. 2000). In feeding studies, hatchling lizards maintained positive growth rates on a diet of just a single native ant species (*Crematogaster californica*), but failed to gain weight when fed a diet consisting exclusively of Argentine ants (Suarez & Case 2002). These findings and other behavioral and physiological evidence (Suarez & Case 2002) suggest it will be difficult for horned lizards to successfully shift their diet away from native ants, which indicates a strong, deterministic link between the decline of horned lizards and Argentine ant invasion.

In other geographic areas within the introduced range of the Argentine ant, ecological consequences of invasion are equally dramatic. In Australia and South Africa, displacement of native seed-dispersing ants results in breakdown of existing seed-dispersal mutualisms and leads to a reduction in native seed dispersal and shifts in the composition of communities of native plants (Christian 2001; Rowles & O'Dowd 2009). Also in South Africa, the arboreal presence of Argentine ants threatens to disrupt the reproductive cycle of insect-pollinated plants as floral arthropod diversity and abundance is reduced (Lach 2007, 2008). In Hawaii invaded arthropod communities experience strong functional shifts in terms of trophic structure and total arthropod biomass (Krushelnycky & Gillespie 2008).

The linear and fragmented design of the Orange County reserve system underlies the reason for its high level of vulnerability to invasion by Argentine ants. At the time of planning, incorporating considerations for edge effects was considered key to successful design of nature reserves (Wilcove et al. 1986; Laurance 1991). When reserves are small or irregularly shaped, edge effects are especially powerful forces that reduce the effective size of a reserve in proportion to the distance to which they penetrate (Murcia 1995; Laurance 2000). Through application of the core-area model (Laurance & Yensen 1991), we were able to determine the degree to which the Orange County reserve system deviates from an optimal design with respect to edge effects. The core-area model uses a shape index (SI) and information on the distance to which edge effects penetrate natural areas to calculate the "affected area" of a reserve. For comparative purposes, if the reserve were a perfect circle, then the SI value would be 1.0 and the area affected by Argentine ants would be limited to 860 ha (6% of the total area). If the SI value were 2.5, which is considered a more realistic value for real-world reserves (Laurance 2000), the affected area would equal 2162 ha (14%), which is still substantially below the 44% affected area we identified. Clearly, the degree to which the Orange County NCCP incorporated considerations of edge effects during the planning process was limited and has resulted in a reserve system that is highly vulnerable to edge effects that penetrate 200 m or more into reserved areas.

Social, political, and economic constraints will always restrict the size, number, and configuration of reserves established as part of an HCP. It is because of these constraints that the best-possible science needs to be applied to the conservation planning process. As noted by Rahn et al. (2006), and evident from the results of our present study, it is not enough for HCPs to rely on the assumption that simply protecting designated natural areas from development will result in protection of associated species or ecosystem functions. If HCPs are to fulfill their conservation promise, a more-integrated and systematic approach to the habitat conservation planning process is needed. A significant body of scientific theory and application is available to provide material for the construction of successful conservation policies (Margules & Pressey 2000; Hierl et al. 2008; Regan et al. 2008). As more empirical studies evaluating the effectiveness of existing HCPs are completed, the need to apply this knowledge will likely become ever more apparent.

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Supporting Information

Geographic distribution of the ant species collected across the study area is available (Appendix S1) as part of the online article. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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